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The Anatomy of *Phoradendron villosum* Nutt.

BY W. A. CANNON

(WITH PLATES 27, 28)

The California species of the American mistletoe (*P. villosum*), in the vicinity of Stanford University, is found on several kinds of evergreen and deciduous trees, among which are the following: Common locust (*Robinia pseudacacia*), Lombardy poplar (*Populus nigra*), species of willow, and the Roble, Douglas, Encina, and Kellogg oaks (*Quercus lobata*, *Q. Douglasii*, *Q. agrifolia* and *Q. Kelloggii*) and it has been reported from Chico, California, as occurring on the cultivated peach. The parasite is abundant on the Roble oak, and since the latter is common in the vicinity of the university, it was chosen to study as the host.

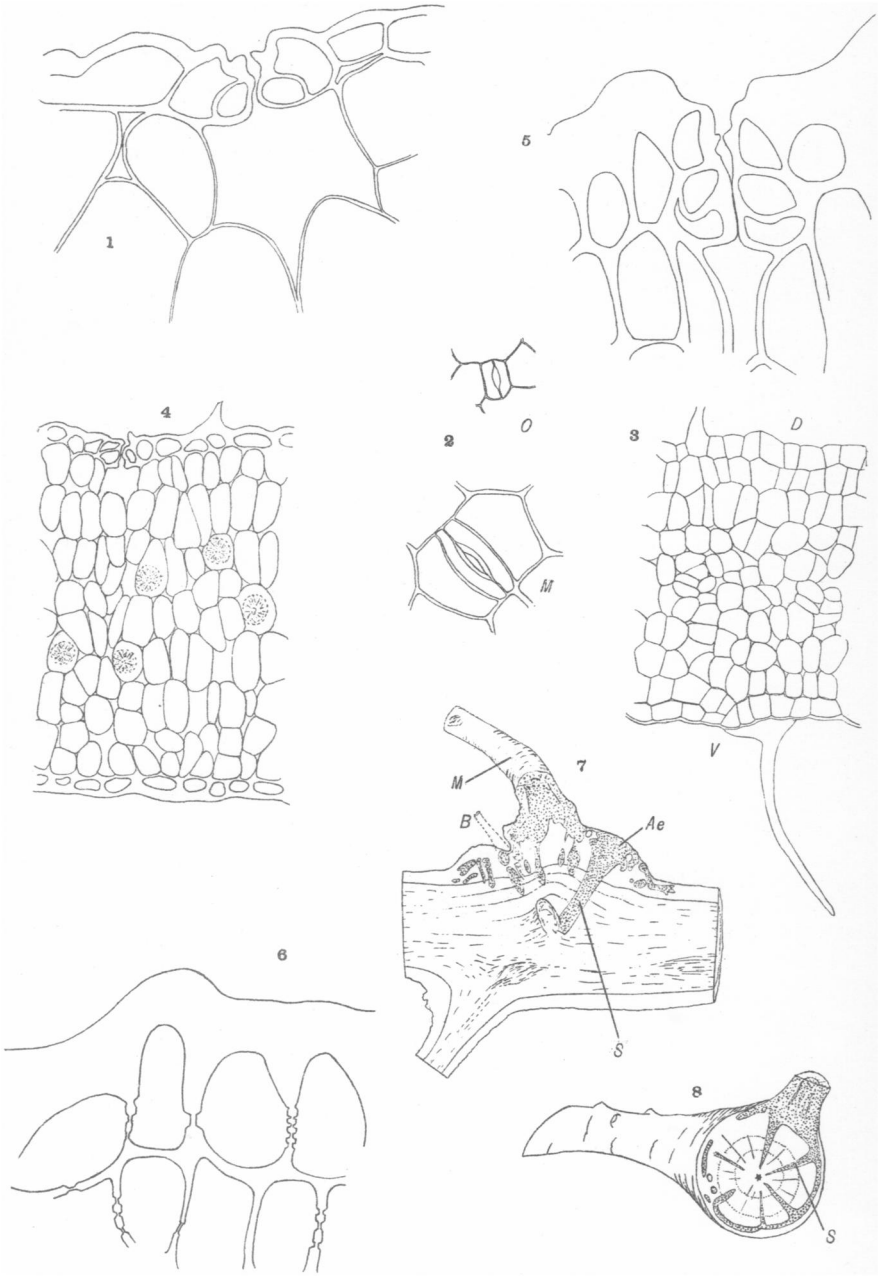
The present paper deals merely with the anatomy of the mistletoe, but it is intended that it shall be followed as soon as convenient by a contribution from the Botanical Laboratory on the biology of the plant.

The material was collected mainly in the spring and early summer of 1899. It was killed with alcoholic corrosive sublimate, and all of the sections were cut by hand.

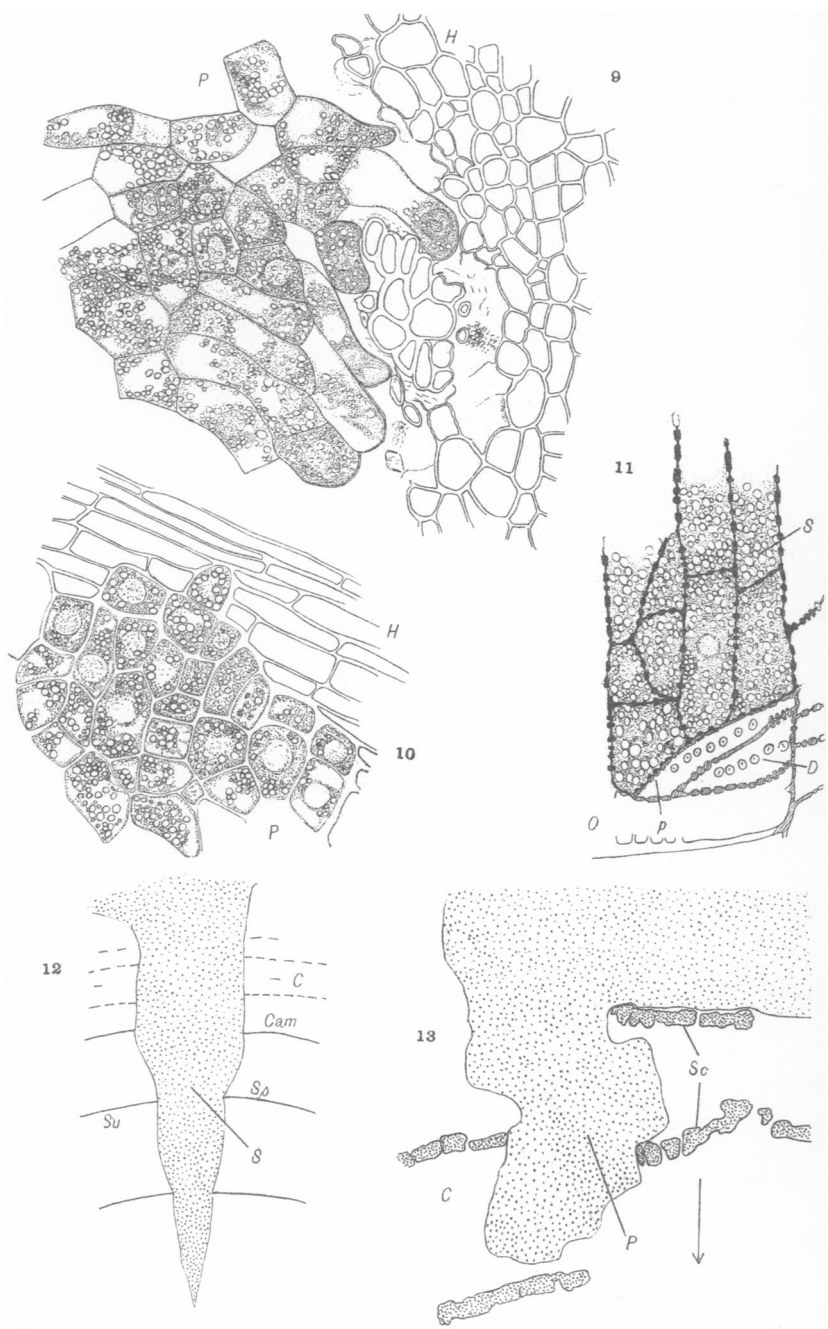
This study was carried on under the direction of Dr. G. J. Peirce, to whom I take pleasure in expressing my gratitude for his great helpfulness in this, and in other work.

I. THE LEAF

The leaves of the mistletoe are borne in alternating pairs on stout stems, which arise from the host at varying angles in respect to the horizon, and consequently in reacting to the light, the leaves assume a more or less vertical position and become bent in petiole and blade. They are relatively thick, of a yellowish-green color, and are markedly brittle. There is a regular gradation in the size of the leaves throughout the younger portion of the plant, so that it is impossible to assign most of them to a definite season's growth. The mature ones measure 3.25-4 cm. in length by 2.5 cm. in



PHORADENDRON VILLOSUM



PHORADENDRON VILLOSUM

breadth. The youngest leaves which may be seen in early spring measure .3 by .75 cm., while the next older ones are 1-1.25 by 1.75-2.25 cm. There is a like difference in measurement between the second and third sets of leaves, and also, the differences in area of the first two seasons' leaves are generally paralleled by a difference in thickness. The leaves do not increase in thickness after the second season.

The tips of the youngest leaves are projected beyond the growing point of the stem, and their dorsal surfaces are closely pressed together. The surfaces thus in contact are inaccessible to the light and are colorless, while exposed surfaces take on the color characteristic of the plant. A cross section of such a leaf shows that it has a well-defined epidermis, and a mesophyll composed of similar cubical cells with small intercellular spaces. The cuticle of the dorsal surface is noticeably thinner than that of the ventral (Fig. 3) and this, like the coloration, may be in some manner associated with the length of exposure to the light. A relatively large number of epidermal cells on both sides of the leaves are prolonged into long trichomes with bulbous bases, and both trichomes and epidermal cells are well filled with finely granular protoplasm and are provided with large nuclei. The cells of the mesophyll, in the second season, become elongated and palisade-like, and it is to the lengthening of the mesophyll cells in a direction at right angles to the surface of the leaf, that the increase in thickness, spoken of above, is due. (Fig. 4.) In this regard *P. villosum* recalls *Viscum album*.* The increase in thickness from the first to the second season is as the ratio 1 : 2.† The measurements are .4 mm. for the first, and .79 mm. for the following season. As the leaves mature the cell walls become pitted, a large number of them are found with crystal aggregates (calcium oxalate), and prominent intercellular spaces are developed. Another characteristic of the old leaf is the kind and position of the stomata. The stomata, which are found on both sides of the leaves, are of the xerophytic type described and figured by Schimper,‡ and while they are con-

* Marktanner-Turneretscher, Sitzungs. d. k. Akad. d. Wissen. Math.-Natur. Classe, 91 : 5 Heft, May, 1885.

† Warming, Pflanzengeographie, 302.

‡ Schimper, Pflanzengeographie, 7.

siderably sunken beneath the surface they are less so than those of the stem. In comparing the stomates of the mistletoe with those of the oak in regard to size and number, it is found that those of the former are about twice as large (Fig. 2) and only approximately half as many to a given area as those of the latter. The number of stomates per square millimeter on each surface of the mistletoe leaf is about 40, while on the oak, where they occur on one side only, there are about 80.

The conductive system of the leaf is poorly developed and the tracheids at the ends of the leaf traces are not swollen as in *Loranthus*, and to some extent in *Viscum*.^{*} No water reservoirs, such as are described by Marktanner-Turneretscher for *Viscum*, the presence of which is denied by Solereder,[†] are to be found in *P. villosum*.

The color given to the mistletoe by the cuticle, which was spoken of above, has led to a supposition that there is a peculiar quality of chlorophyll in the plant that is in some manner associated with its parasitic habit. This is not at all the case. The external color of the plant is entirely due to the coloration of the cuticle, and the chlorophyll, as far as I could determine, was quite normal. I tried to dissolve out the coloring matter from the cuticle by using the common solvents and thus learn its nature, but in this I was quite unsuccessful.

The leaf of the mistletoe is mechanically very weak. This is partly due to the poor development of supporting tissue, but chiefly to the prominent intercellular spaces. If a leaf is broken in two, and sections are cut at right angles to the fracture, it will be seen that the line of fracture passes between the cells, or that, in other words, it coincides with the intercellular spaces. It is likely here as in the stem that perhaps the main element of strength lies in the unusual development of the outer epidermal wall, the cuticle. This will be spoken of again later in this paper.

2. THE STEM

A cross section of a young stem shows a wood cylinder made up as usual of conductive tissue, medullary rays, wood paren-

^{*} Marktanner-Turneretscher, l. c.

[†] Solereder, Anatomie der Dicotyledonen.

chyma, and pith, and also, a cortex with a well-defined epidermis. The young epidermal cells are cubical in form, but as the stem increases in diameter they and the underlying cells for some distance become much flattened. The lateral and internal walls of the epidermal cells bear numerous pits (Fig. 6). Some of the outer cells project as trichomes and some are modified to form stomata which are deeply sunken in the older parts of the stem (Fig. 5), and are of the xerophytic type, the stomata of which are placed longitudinally.

The cortex of the young stem is composed of thin-walled cells with intercellular spaces. As the stem becomes larger the walls of these cells increase in thickness until in the older parts they are relatively very heavy. They, at the same time, develop numerous pits. The intercellular spaces also in the older stem take on the characters which we have seen to be so pronounced in the leaves. Groups of grit cells and cells bearing calcium oxalate crystals are noticeable characteristics of the old stems.

Within the cortex of the young stem is a ring of several fibrovascular bundles, of the open collateral type, separated by medullary rays. A group of hard bast fibers, which are derived from the pro-phloëm, is found inside of the pericycle exterior to each bundle. Subsequently no hard bast is formed in the stem. Also, on the inside of each bundle opposite the group of hard bast fibers, is another group of hard bast-like fibers. These two groups of sclerenchymatous tissue can be recognized in the old stems although in these they occupy but a small proportion of the entire area. The first definitive wood elements to be recognized are the ringed tracheids, and later reticulated tracheids, which with the growth of the stem become changed into tracheid-like ducts by the reabsorption of the division walls. But the form of the tracheids of which the ducts are composed is clearly recognizable. Associated with the ducts are elongated cells, which become thick-walled and form the wood fibers of the xylem. When these fibers are young they present much the appearance of slime canals. The contents of the fibers give the sugar reaction with Fehling's solution, and in the younger ones, the walls are cellulose. In all old fibers, however, these walls are lignified. If the fibers function as slime canals at any time they probably cease

to do so when the change in composition of the walls takes place. It should be said that the slime canals in *Arceuthobium* are of quite different character, and also that they entirely, or for the most part, occur in the cortex of the stem. Short cells with heavy, pitted walls form the wood parenchyma and constitute a relatively large proportion of the wood elements. Attention may be called here to the structure of the wood cylinder as regards mechanical strength although that will be considered more fully below. The element of strength, the relatively large number of fibers, of the oak stem, is seen to be wanting in the mistletoe, and those kinds of cells which do not contribute primarily to the strength of the stem, the wood parenchyma, and which are present in a small amount in the oak, are again the most abundant in the mistletoe.

The pith of the young stem is composed of cells which are quite like those of the medullary rays and of the cortex, but in the old stem they become heavily walled, and because of the presence of pits, have a peculiarly ragged appearance in cross section. And it should be said that perhaps the most striking character of the stem is the presence in the pith and cortex, mainly in the pith, of heavy walls and of correspondingly deep pits.

The stem of this mistletoe, like the leaf, is mechanically very weak. A comparatively small amount of force is needed to snap it in two, and this weakness is in a measure independent of the size of the stem. The reason for the brittleness can doubtless be found in its structure. Among the factors that make for this condition may be counted the great number of crystal-bearing cells, the large number of grit cells, the presence of prominent intercellular spaces, and of deep pits in the walls of the parenchymatous cells. And to these may be added also the absence of secondary bast fibers, the small number of wood fibers present, the peculiar tracheid character of the wood ducts, and the relatively large amount of xylem parenchyma. The greatest single source of strength is probably the outer wall, the cuticle, of the periderm. If the cuticle is carefully removed for a short distance, say 5 cm., from a portion of the stem, the end of which is firmly secured, and weights are placed on the free end, the stem will bend and finally break in the region from which this has been removed. The influence of the weights will hardly be observed in other parts of

the stem, and will scarcely affect a similar one from which the cuticle has not been removed. Further, if the fracture of the mistletoe stem be compared with that of an oak a difference characteristic of the structure of the two may be seen. The mistletoe stem breaks straight across with no tendency to split, while the oak breaks irregularly and splits at frequent intervals.

3. THE HAUSTORIA

The mistletoe is attached to its host by haustoria, which in structure and in function show evident differentiation. The young haustoria ramify in all directions in the cortex of the host and they may even quite encircle the central cylinder.* From these others turn sharply toward the center of the host branch, and become partly enclosed by it. These latter are the so-called sinkers of the parasite. Upon a considerable increase in diameter of the cortical haustoria, the cells of the cortex of the host, which are outside of the haustoria, gradually loose their contents and die and the haustoria are in this manner exposed to the air. They undergo considerable change in structure in the meantime. There are thus three easily distinguishable sorts of haustoria, which, for convenience I shall refer to as cortical haustoria, sinkers, and aërial haustoria.

The youngest cortical haustoria are composed throughout of thin-walled parenchyma. All of the cells are densely filled with a coarsely granular material which gives a starch reaction. While the cells of the interior of the haustoria are pretty much alike, those corresponding to the epidermis are somewhat differentiated. In some portions of the haustoria the outer cells appear much like typical epidermal cells, and in others, at the growing parts, they are much elongated and are papilla-like (Fig. 9). The latter recall those in the region of the young haustoria in the dodder,† as well as the epithelial cells in the scutellum of grasses,‡ and they appear to have a function analogous to both. The elongated cells of the mistletoe haustoria secrete a solvent that is capable of digesting

* In *Viscum* the haustoria do not surround the stem of the host. Kerner and Oliver, *Natural History of Plants*, 208.

† Peirce, *Annals of Botany*, Sept., 1893.

‡ Lermer and Holzner, *Beiträge zur Kenntniss der Gerste*. Munich, 1888.

most, although it would seem not all, of the cortical tissues of the host. These cells contain finely granular protoplasm, and nuclei which are larger than those in the interior of the haustoria. The host cells which are adjacent to those of the haustoria are rich in food material and they stimulate to great activity the epithelial haustorial cells just described. The adjacent host cells show evident signs of breaking down, and usually a small space intervenes between them and those of the parasite. It has already been stated that the epithelial cells appear to be unable to dissolve certain of the host tissues; these are the sclerenchyma of the oak. The form and size of the digestive cells vary with the changes in structure of the host cells. The former are relatively long when the host tissues furnish them with an abundance of food, but they become short and cubical when the adjacent host cells are poor in food as, for instance, when they are near the surface of the host stem. In the latter case the epithelial cells insensibly merge into the more typical epidermal cells. Not only is the shape and size of the epithelial cells dependent on the character of the adjacent host tissue, but it will soon appear that the ramifications of the haustoria through the cortex are also dependent on the same factor, because the epithelial cells make clear the way for the advancing haustoria.

The tissues within the epidermis of the cortical haustoria become differentiated early into a central conductive system and a surrounding cortex. The cortex is composed of thin-walled cells with intercellular spaces. These cells, like those of the cortical haustoria in general, except the conductive system and the epithelium, are well filled with coarse grains of starch. Grit cells are present in the cortex, but it is not possible in every case to say whether they originated in the cortex of the host or that of the parasite. Sections of young cortical haustoria frequently show numerous masses of fully-developed grit cells in the midst of young and thin-walled parenchyma, and such grit cells have been surrounded, but not digested by the epithelial haustoria cells and come finally to lie wholly within the tissues of the parasite.

The conductive tissues of the cortical haustoria are developed late and possess elements which resemble analogous portions of the stem. Ducts appear in what may be termed the central cylin-

der, and cambiform cells occur between the cylinder and the cortex. The cortical haustoria do not begin secondary growth until they cease to function as food absorbers and serve the parasite as food conductors, and to some extent as food reservoirs. With this change in function appears a change in structure, and the cortical haustoria pass over into the aërial haustoria which will be spoken of later.

Before examining the structure of the haustoria of the mistletoe further it will be best to briefly glance at the main characters of the structure of the host branch (Roble oak, *Quercus lobata*) on which the parasite grows.

The oak branch is made up of a central cylinder surrounded by a cortex. The cylinder is composed of a relatively large number of fibers, of a small amount of wood parenchyma, of radiating medullary rays, and intermingled with other wood elements, especially in spring wood, are also large and small tracheae, or ducts. The wood parenchyma and medullary rays are living cells and are well supplied with food. The ducts are lifeless and serve for the transport of food materials in solution, which have been taken by the roots of the host plant. Most of the prosenchyma cells have scarcely any lumen and are lifeless, and it may be said in passing that the oak owes its strength to the relatively great amount of wood fibers of the wood cylinder. As indicated above, the wood fibers of the mistletoe are present in relatively small numbers, and in this connection a comparison of the two sorts of stems is of interest.

The cortex of the oak is made up of small parenchymatous cells which are compactly set together, of several concentric rings of sclerenchymatous fibers arranged in groups, and of scattered grit cells. Instead of an epidermis, as in the mistletoe, the oak has a few layers of cork which are derived from a superficially placed cork cambium. A meristematic zone of cells, the cambium, separates the cortex from the central cylinder. The outer fibers are lignified, but the inner are not uniformly so. The grit cells are also lignified. Of these tissues, the parenchyma and the meristematic region are richly supplied with food, and it is among the cells of these that the cortical haustoria of the parasite ramify.

Taking up now the growth of the haustoria in the cortex of

the host and their later development into sinkers, it will be seen that the haustoria seek only those cells which contain food; they are chemotactic, and this may be called the positive element in the growth of the haustoria. The negative element is found in those host cells which are either poor in food, or furnish mechanical resistance to the progress of the haustoria, or both. The cells toward the periphery of the branch would represent the first, and the grit cells and fibers the second conditions. How masses of grit cells may affect the growth of the haustoria has already been touched upon. It was found, however, that owing to the characteristic form of these cells the haustoria could envelop them with their own tissues and flow past them, the course of growth not being changed by their presence. The case is somewhat different in regard to the fibers in the cortex of the oak, and they are an important factor in directing the growth of the cortical haustoria as well as those haustoria which penetrate into the xylem of the host. The position and number of sinkers are to a great degree, and perhaps wholly, controlled by the permeability of the inner ring of fibers to the haustoria. From the outer cortical cells of the host the haustoria grope between masses of fibers which compose the outer ring of sclerenchyma to the parenchyma within (Fig. 13), and in a similar manner through the second and each ring of fibers and parenchyma in succession until the inner ring is reached, and the haustoria pass between the gaps in this ring and penetrate the bast and become transformed into sinkers. In every instance the haustoria pass from an area poorer in food to one richer, and they are led in this manner to a position opposite the medullary rays so that with an increase in diameter of the host stem they are in position to supplant them. Such in brief is the origin of the sinkers.

A young sinker is in no respect different from any other part of a cortical haustorium. It originates on that part toward the wood cylinder and, as has just been stated, becomes a sinker by penetrating between some gap in the inner fiber ring of the host cortex. When the phloëm of the host is reached, and especially the cambium, the cell walls of the sinker become somewhat heavier and the end cells shorter than corresponding ones of the cortical haustoria (Fig. 10). The host cells just in front of the tip of the sinker in the cambium or in the bast present a curved appearance as if under pres-

sure. It is not likely that the sinker absorbs the adjacent tissue of the host to any extent because no evidence of this was seen, and, further, there is an absence of epithelial cells, or of cells having that general character, in the sinker. The cells of the young sinker which correspond in position to epithelial cells of the cortical haustoria are cubical, and thick-walled. No cells in mature sinkers exhibit epithelial characters; the change in structure and in function of these cells takes place in the meristematic region of the host.

A cross section of an oak branch to which a mistletoe is attached shows that the sinkers of the parasite take the position of the host's medullary rays, and that the structure of portions of the sinker varies according to their relative positions. The part of the sinker which is in the cortex of the host agrees very well in structure with the cortical haustoria, but that portion which is within the xylem has a different and a characteristic structure. The sinker taken as a whole is composed of a central cylinder and a surrounding cortex. The central cylinder is, in both portions of the sinker, an almost uniform structure, but the cortex is variable. The cortex of that part of the sinker that is within the cortex of the host is composed of thin-walled cells and has few intercellular spaces. On the other hand, the outer part of the sinker cortex, which is within the wood cylinder of the host, has a denser structure, and is made up of heavy-walled cells with no intercellular spaces. The inner portion of the same part of the cortex is composed of thin-walled cells between which there are small spaces. Between the two sorts of sinker cortex just spoken of, and in a position approximately adjacent to the host cambium is the meristematic portion. Here the cells are brick-shaped, relatively small, and there are no intercellular spaces. The contents of the sinker cells appear to be almost entirely composed of starch in character resembling that of the cortical haustoria. The cells of the sinker cortex remain alive in the oldest material that I examined, and they probably die only as the parts of the host adjacent to them die. The walls of all of the sinker cells which are within the cortex of the host are lignified.

The conductive tissue of the sinker is composed of a few spiral and annular ducts which are enclosed by narrow, elongated thin-

walled cells. The latter are densely filled with finely granular matter the nature of which I did not learn. I did not succeed in demonstrating the presence of sieve tubes in the sinkers; their existence may be questioned. The long, thin-walled cells of the central cylinder are gradually shortened, and their walls thickened, as they approach the end of the sinker, and they are there indistinguishable from the other cells that make up the tip. The ducts also, at the end of the sinker, merge into the cells that compose it, so that there is a gradual transition from the cells of the central cylinder to those of the end of the sinker. The cells at the end and on the margin of the sinker are in contact with the host ducts and the union is such a close one that there is apparently only one cell wall between them. The pits of the sinker are in apposition with those of the ducts (Fig. 11) and the status of the parasite as a partial, or water, parasite, is thus established.

In the region of the cambium of the host, as has already been mentioned, the sinker cells are smaller and with thinner walls than those either toward or away from its tip. These cells have large nuclei and dense protoplasmic contents. They are typical meristematic cells. The thickness of this part of the sinker is somewhat more than that of the cambium of the host adjacent to it. By the means of active cell division in the meristematic region of the sinker it is able to accommodate its length to the increasing diameter of the oak branch. And it is also possible that the elevation of the aërial haustoria from the host is in part accomplished by the same agency.

Longitudinal and cross sections of the sinker in the region of its meristem show that the thin-walled conductive system does not unite with the phloëm of the host, sieve-tubes do not unite with sieve-tubes as in complete parasites. There is, however, a transfer of foods from the phloëm of the host to the sinker as in the cortical haustoria, but it takes place by osmosis only, because there do not appear to be any cells of the sinker with epithelial characters. The sinker, because of the lack of cells for digestive purposes, does encroach upon the phloëm of the host. This is shown by longitudinal sections (Fig. 12).

The aërial haustoria are those cortical haustoria which have become more or less freed from the host cortex, are partly or

wholly exposed to the air, and have undergone marked changes in structure and in function. As the cortical haustoria increase in bulk and occupy a larger and larger area in the host cortex, the flow of foods and food materials from the central to the more peripheral portions of the cortex is gradually checked, and the outer cells of the host cortex die. The inner cells of the host cortex, however, remain alive, and may form cork cambium between the aërial haustoria and the xylem of the host. By the multiplication of the cortex cells beneath the aërial haustoria, a considerable pressure is brought to bear upon the haustoria, which is exerted in such a way as to tend to push them away from the host branch. A flattening beneath the haustoria of the host cortical cells in question shows this point very plainly.

Parallel to the decadence of the superficial host tissues a change is noted in the structure of the cortical haustoria. This is first seen in the epidermis. The outer walls of the epidermis become greatly thickened and take on the bronze color peculiar to the exposed portions of the plant. This, especially the latter, applies to the parts of the epidermis which are exposed to the air. In sections through the edge of the dying cortex and also through the epidermis of the haustoria, the formation of the cuticle as well as the deposition of the coloring matter in it, under the influence of the light, may easily be seen. Except for the greater irregularity, the absence of trichomes and of stomates, the epidermis of the aërial haustoria agrees very well with that of the stem.

The structure of the cortex of the aërial haustoria is also in the main like that of the stem, but the cells of which it is composed are more irregular in form and in size. Grit cells and crystal-bearing cells are present in the cortex.

Cross sections of the wood cylinder of the aërial haustoria have a striking appearance, which is caused by the unsymmetrical growth of its members, the secondary growth in diameter taking place on one side, toward the outside of the stem of the host, more than on the other. The elements of the central cylinder of the haustoria resemble those of the stem, but the pith, the primary vessels and the central ring of sclerenchyma are wanting. The peculiar structure of many of the fibers, by which they resemble slime canals, and which was spoken of as occurring in the stem,

appears in the wood cylinder of the aërial haustoria. However, in the latter case the canals appear to be permanent. This point needs further investigation.

The phloëm consists of bast parenchyma, of sieve tubes, and companion cells. The sieve plates were difficult to demonstrate. The primary hard bast bundles, typical of the stem, are, of course, not found in the haustoria.

In comparing the mass of cortex with the mass of conductive tissue in the cortical haustoria with the same in the aërial haustoria we see a decided difference—the cortex preponderates in the former, the conductive tissue in the latter case. This is correlated with the change which these haustoria have undergone in function. An index of this change is found in the contents of the cortex of the two sorts of haustoria. Starch grains are found in the cortex of the cortical, but they are not present to any appreciable extent in that of the aërial haustoria. That is, the cortex of the aërial haustoria has ceased to function as a food reservoir. The gréat development of conductive tissue is also indicative of the change from an absorbing organ to a conductive one.

In concluding this account of the haustoria of the mistletoe it should be said that each of these kinds of haustoria are present in the older plants as well as in the young, and in this regard the American mistletoe does not agree with the European species (*Viscum album*). In *Viscum* there is a sort of tap root from which the lateral roots, cortical haustoria, spring. Frank* does not mention the formation of aërial haustoria in *Viscum* and he intimates that such, indeed, are not present, because he says that the connections between the sinkers and the stem, the aërial haustoria, are sooner or later broken. Although I have not made a close study of the oldest plants, I believe from the manner of the formation and development of the aërial haustoria that in the American mistletoe that connection during the life of the plant is never broken. This must necessarily be the case since the aërial haustoria become an integral portion of the stem.

* Frank, Die Pflanzplanzen, Krankheiten der Pflanzen, 1896, p. 530.

4. SOME BIOLOGICAL CONSIDERATIONS

In concluding this sketch of the anatomy of the mistletoe it need hardly be pointed out that, whatever may be the nature of the stimuli, varying pressures or what not, which bring about the characteristic structure of the mistletoe, it is for the most part typical of xerophytes in general. It is to be pointed out however, that the extremely heavy walls of the parenchyma is a feature found in many leaves, and stems of herbaceous species, which live through one or more winters, or inclement seasons. Similar structures are to be seen in coniferous leaves, as well as in leaves of some orchids such as *Aplectrum*. It is also to be said that such strength of wall would give rigidity to the stem during seasons in which turgescence in these cells is an impossible condition.

In the consideration of the growth of the leaves it was shown that they did not reach the normal thickness until the second season, and the mature size was not attained until an indefinite time after that. The youngest leaves are illuminated from one side, the ventral, only, and Fig. 3 shows very imperfectly that there is a corresponding difference in the time of development of the two parts. The portion toward the light appears to have a structure somewhat more fully differentiated than the opposite side. In the mature leaf both surfaces are equally exposed to the light, and show equal development.

Among the many questions which come up for solution in a study of this kind, and which belong to the purely biological side of the general problem, may be counted those which concern the nature of the association of the mistletoe and the oak. Is the relationship between the two entirely of advantage to the parasite, or does the oak also derive benefit from it as is apparently the case in *Viscum album*?* It is clear that at the season of the year when the oak leaves have fallen, and when the plant no longer makes food, the mistletoe might be called upon to give up a portion of the food, which it was manufacturing, to the support of the host. As far as I could learn, however, such is never the case. Material collected at such a time was examined and it was found

* Gaston Bonnier, Sur l'assimilation des plantes parasites à chlorophyll, Comptes Rendus, Paris, 113: 1074-1076.

uniformly that those parts of the parasite which are the reservoirs of food contained apparently the usual amount, and that the adjacent oak tissues did not show in any way that food passed to them in the manner described. When the structure of the parasite and its relation to the oak are considered it will appear that there is really little opportunity for such a transfer of foods. The parts of the mistletoe that contain food are either in contact with the lifeless host cells (the ducts of the wood), or they are adjacent to host cells which, at the time, are dormant.

The usual conception of the mistletoe as a semi-parasite, or a water parasite, is for the most part a perfectly correct one. But the degree of parasitism varies with the age of the plant, and with the portion of the plant under consideration, for although the main part of the parasite lives on the water and the mineral salts in solution which it gets from the conductive system of the host and the carbon that it gets from the air, a small portion of the cortical haustoria depends upon the host entirely for its food and is therefore totally parasitic. The first assertion, that the degree of parasitism varies with the age of the plant, remains to be demonstrated, but there seems little question that the seedling is a total parasite, just as the cortical haustoria are. In this connection it may be of interest to point out how such a total parasite as *Arceuthobium* may have arisen. *Arceuthobium* lives in the cortex of its host, it gets food already elaborated, and its only appearance in the air is when it sends out the fruiting stalks. Now, if the American mistletoe should acquire the habit of remaining a longer and longer time after germinating in the cortex of the host, either because of difficulty in penetrating the xylem of its host, or for any other reason, it might gradually lose its power of carbon assimilation and become a total parasite like *Arceuthobium*.

The immediate effect of the parasite was not studied, but the ultimate effect, in all cases that came to my notice, is to cause the death of that part of the host which is beyond. There does not, however, appear to be any such striking malformation as in the *Arceuthobium*, or in another species of *Phoradendron* that grows on the juniper (*P. bolleanum*). *Viscum* also causes the decay of the host tissues and in this resembles *Phoradendron villosum*, but the effect is brought about in quite a different way. In *Viscum* the

sinkers that have severed their connection with the main part of the parasite through the death of the cortical haustoria, so choke the passages of the host's conductive system that growth ceases and it eventually dies from starvation.* In the American mistletoe, on the other hand, the destruction of the host tissues is brought about by the living sinkers which, while still attached to the cortical, now become the aërial haustoria, occupy the places of the medullary rays (Fig. 8) and absorb so much water that the more distal portions of the host are starved. The position which the American mistletoe often occupies at the extreme tip of a limb is brought about in the manner described with the further note that the parasite may extend its haustoria to include within its grasp the branch of which the one on which it germinated was an offshoot (Fig. 7).

COLUMBIA UNIVERSITY, March 13, 1901.

Explanation of Plates

PLATE 27

1. A cross section of a leaf the same age as the leaf of Fig. 4, showing a stomate, $\times 220$.
2. Surface view of stomata to show the relative size: *O*, oak, *M*, mistletoe, $\times 220$.
3. A cross section made in April of a leaf of the first season: *D*, dorsal surface, *V*, ventral surface, $\times 76$.
4. A cross section of a leaf of the second season made in the spring before the growth in diameter was completed. A few cells with calcium oxalate are shown, $\times 76$.
5. A cross section of a stem of the same age as that of the following figure, with a characteristic sunken stomate, $\times 220$.
6. A section of a rather young stem showing the great development of cuticle, $\times 320$.
7. Oak branch and mistletoe attached: *m*, mistletoe; *Ae*, aërial haustorium; *b*, the branch upon which the mistletoe germinated, the end of which is indicated by the dotted lines. Two thirds natural size.
8. A cross section of an oak branch with a mistletoe. The cortical haustoria have surrounded the wood cylinder of the oak, and sinkers penetrate it from every side; *S*, sinkers, $\times (ca) 2$.

PLATE 28

9. A section through the epithelial region of a cortical haustorium; *P*, parasite; *H*, host, $\times 220$.

* Frank, *I. c.*

10. A longitudinal section through the bast of the oak and the tip of a young sinker, the cells of which have for the most part lost their epithelial characters : *P*, parasite ; *H*, host, $\times 220$.

11. A longitudinal section of the tip of a sinker, radial of the wood cylinder of the oak, which shows the apposition of the pits in the walls of the ducts and in those of the outer cells of the parasite : *S*, sinker ; *O*, oak ; *D*, ducts of oak ; *p*, pits of host and parasite in apposition, $\times 320$.

12. A longitudinal section, partly diagrammatic, of sinker, cross section of the oak, showing the effect of the season's changes in pressure of the oak wood cylinder ; *S*, sinker ; *C*, cortex of oak with the fiber rings indicated by dotted lines ; *cam*, oak cambium ; *Sp*, spring ; *Sn*, summer wood.

13. A partly diagrammatical sketch of cortical haustorium in oak cortex. The arrow points to the center of the oak stem : *P*, parasite ; *C*, oak cortex ; *Sc*, sclerenchymatous cells.